

Comparative Rate of Respiration in Some Earthworms (*Lumbricidae*, *Oligochaeta*)

J. B. BYZOVA

LABORATORY OF SOIL ZOOLOGY (LABORATORY LEADER - PROF. DR. M. S. GHILAROV)
INSTITUTE OF ANIMAL MORPHOLOGY, USSR ACADEMY OF SCIENCES, MOSCOW

Data on the metabolic rate in the invertebrates are ever more utilized for calculations on the energy of biological processes in nature, in the soil in particular (HEMMINGSEN, 1960 ; MACFADYEN, 1961 ; ENGELMANN, 1961 ; PHILLIPSON, 1963). The metabolism of invertebrates turns out to be directly related to soil fertility (FRANZ, 1951 ; MACFADYEN, 1961). The mean data on large taxonomic groups, or those on individual representatives are usually applied as the indices of the rate of metabolism of a given groups as a whole for theoretical calculations and for the establishment of general regularities. However, a study of the variation within the ranges of general regularities always preserves its interest. Thus, the knowledge of the metabolic specificity of individual components of the biological system analysed is required for a characteristic of metabolic processes going on in the given conditions (forest type, various arable plots, etc.).

In this connection a study of the metabolism, in particular, the respiratory metabolism in the earthworms is of great interest since Lumbricids are one of the most important groups by their biomass and by the part they play in soil formation. The respiration of the earthworms was studied by many authors. Their attention was mainly attracted by the role of hemoglobin in relation to the ability of the worms to survive a long period oxygen lack. Temperature effect upon the rate of oxygen consumption was also studied. A comprehensive critical review of the literature on the respiration of Lumbricid was published by MENDES and ALMEIDA (1962). Many data on respiration were also included in the monograph of LAVERACK (1963) devoted to the earthworm physiology. Yet, as pointed out by MENDES a. ALMEIDA, and earlier by WINBERG (1950, 1956), the data presented in a survey of papers are often

incomparable due to different methods applied and to the absence of statistical test of experimental data. Therefore a clear idea of whether taxonomic position or ecological specificity of respiration rate does exist in Lumbricids and of how it depends upon body size is lacking up to the present. The present paper is aimed at the elucidation of these problems. It summarizes the results of observations on the rate of oxygen consumption in several earthworm species differing in their ecology, in their role they play in the process of soil formation and in their zonal distribution.

MATERIAL AND METHODS

The work was carried out on the following earthworm species: *Eisenia rosea* (Savigny), *Allolobophora caliginosa* (Savigny), *Lumbricus terrestris* L., *Lumbricus rubellus* Hoffmann, *Lumbricus castaneus* (Savigny), *Dendrobaena octaedra* (Savigny), *Eiseniella tetraedra* (Savigny), *Octolasion lacteum* (Oerley), *Eisenia foetida* (Savigny). This list includes earthworms belonging to different ecological groups (BALUYEV, 1950; BALTZER, 1956; PEREL, 1963) *Allolobophora caliginosa* and *Eisenia rosea* are dwellers of deep soil layers (low horizons). *Lumbricus rubellus*, *L. terrestris* and *Octolasion lacteum* are inhabiting in mid-strata but, in wet conditions they may pass to upper soil layers and into the litter. *Dendrobaena octaedra* and *Lumbricus castaneus* are litter dwellers, or are to be found just under the litter. *Eiseniella tetraedra* is an amphibiotic species, while *Eisenia foetida* is a compost dweller. Prior to the beginning of measurements the worms were kept in vials, individuals of each species being maintained separately in a substrate drawn at the site where animals have been collected, corresponding to ecological requirements of a given population. For example, *Allolobophora caliginosa*, *Eisenia rosea*, *Lumbricus terrestris*, *L. rubellus*, *Octolasion lacteum* were kept in vials with a large amount of soil, for two latter species sod was also added. *Eisenia foetida* specimens lived in a vial with soil covered by a layer of leaf compost. In the cage with *Lumbricus castaneus* the soil was covered with the sod, while that in the vial with *Dendrobaena octaedra* was covered with a layer of needle = and leaf litter. The soil with *Eiseniella tetraedra* was kept wet, while in other vials no excessive moisture was allowed. The cages with the earthworms were kept in a shady premise at a temperature of 17-20°. Measurements of respiration rate were carried out in at temperature about 19° C.

The rate of oxygen consumption by different earthworms was determined manometrically, using Warburg apparatus, at a constant temperature, in the dark. The measurement procedure was, in principle, similar to that described by MENDES a. ALMEIDA (1962). The only difference was that all measurements were carried on mature and fed earthworms. Utilization of starving worms seemed unadvisable for our aims, since the effect of starvation upon the worms widely differing with respect to feeding habits (PEREL, 1963; SEMENOVA, in press) must vary. The data, although scarce, to be found in the literature support this view. It is shown, for example (NEEDHAM, 1957), that *Eisenia foetida* releases much more ammonia during starvation than *Lumbricus terrestris*, and that oxygen consumption of fasting *Eisenia foetida* makes about 70 per cent of the O₂ amount consumed by feeding worms (KIRBERGER, 1933).

To avoid possible errors in calculations of the respiratory rate on the account of ballast weight of intestine contents the necessary correction for weight was made. This weight was found to be most considerable in the species that continuously passed large amounts of mineral soil particles through their intestine, such as *Eisenia rosea* and *Allolobophora caliginosa*. The mean weight of the intestine contents in both species is circa 10 p. c. of the total body weight. The relative weight of the intestine contents in the species feeding on more concentrated food was less considerable, so that it seemed possible to neglect it.

Only mature individuals were studied as up to now there are no reliable data on the character of respiration rate dependance upon the developmental stage in earthworms. Apart from this, in several instances the identification of immature earthworms by external characters is rather difficult. The measurement of O_2 consumption was carried out on 24-65 individuals of each species. The measurement of O_2 consumption by each individual animal was repeated 2-4 times. The term « replications » in the paper presented implies the number of the means of 2-4 measurements carried out on a single individual. The weight of mature individuals varies greatly. Due to this, maximal weight fluctuations were taken for each species, each weight scale being divided into classes to make the number of repeated observations (replication) equal for each class. For a comparative assay of the metabolic level in different species of Lumbricids the mean values of all the individual measurements are presented. The degree of significance of difference of means is calculated by the accepted biometrical method of the evaluation of difference between the arithmetical means (SNEDEKOR, 1961; ROKITSKIY, 1961; PLOKHINSKIY, 1961). The data on the dependence of the rate of oxygen consumption (per unit of the wet wt. per hour) upon the worm weight were calculated by the least square method.

RESULTS

The earthworms investigated may be divided into two weight groups (table 1). The first comprises: *Dendrobaena octaedra*, *Lumbricus castaneus*, *Eiseniella tetraedra*, *Eisenia foetida* and *E. rosea* whose weight of sexually

TABLE I

Mean rate of O_2 consumption by different earthworm species (in mm^3/g wet wt/h)

Species	Weight, g (W)	Mean resp. rate (q)	Standard deviation ($\bar{C} q$)	Number of repli- cations (n)
<i>Dendrobaena octaedra</i> (Savigny) ..	0,1 -0,36	192	40	60
<i>Lumbricus castaneus</i> (Savigny) ..	0,06-0,42	152	36	42
<i>Eiseniella tetraedra</i> (Savigny)	0,06-0,14	150	43	24
<i>Eisenia foetida</i> (Savigny)	0,09-0,58	95	31	60
<i>Eisenia rosea</i> (Savigny)	0,08-0,59	88	33	65
<i>Allolobophora caliginosa</i> (Savigny).	0,45-1,30	78	16	50
<i>Lumbricus rubellus</i> Hoffmann ..	0,39-1,10	89	29	63
<i>Octolasion lacteum</i> (Oerley) ...	0,65-1,50	75	18	24
<i>Lumbricus terrestris</i> L.	0,56-4,64	74	19	18

mature individuals ranges from 0.06 to 0.6 g, almost equally in all species. *Eiseniella tetraedra* takes a peculiar position in this group being the smallest worm whose weight fluctuations take but a portion of the weight scale mentioned. *Allolobophora caliginosa*, *Lumbricus rubellus*, *Octolasion lac-teum* of 0.4-1.3 g make the second group. *Lumbricus terrestris* being of the largest size were analysed separately.

The mean rate of oxygen consumption (in $\text{mm}^3/\text{g wet wt/h}$) varies considerably in the worms of the first group. The highest mean rate of O_2 consumption was found in *Dendrobaena octaedra*, while the lowest one was observed in *Eisenia rosea*. The weight and the number of replicated measurements being equal, the mean rate of O_2 consumption in *Dendrobaena*

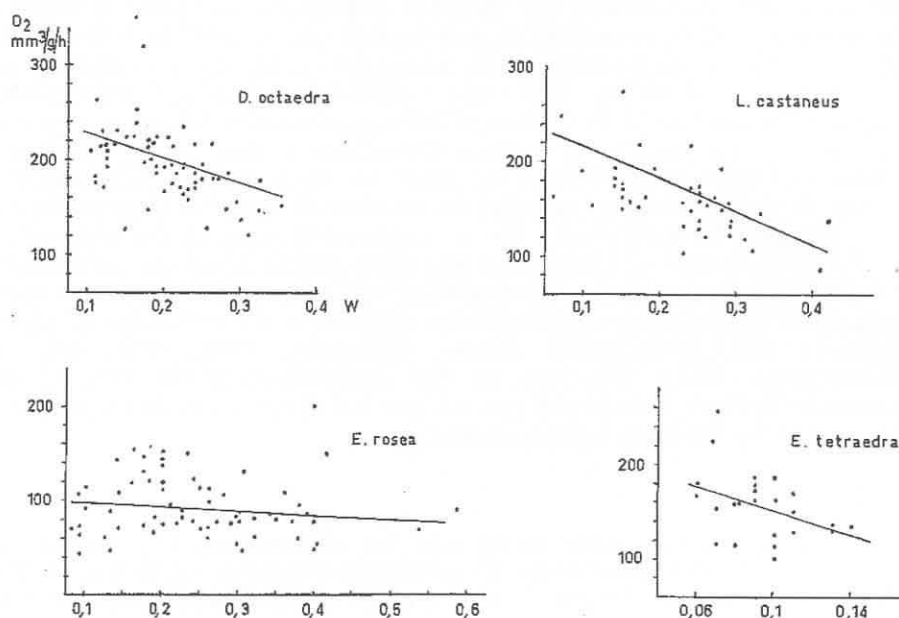


FIG. 2. — Results of measurements of O_2 consumption rate in different Lumbricid species (Abscissa - weight in g; ordinate O_2 consumption in mm^3 per g per h) Straight lines - results of treating experimental data by the least square method.

octaedra was more than two times that in *Eisenia rosea*. Significance of difference, despite great variation of the data of individual observations, is very high ($t = 15$ when $n = 60-65$). It should be noticed that considerable fluctuation of numerical data was shown by all the species investigated which manifests in high values of standard deviations presented in table 1. (All the results of observations on individual species are presented in figs. 2,3).

By the mean rate of O_2 consumption *Eisenia foetida* is close to *E. rosea*. In any case, the probability of small differences observed at the given number of replications is very low. On the other hand, the rate of O_2 consumption by *Eisenia foetida* worms is two times less than that in *Dendrobaena octaedra*, this difference being highly significant ($t = 14$, sufficient value of t being 2.5).

The respiration rates of *Lumbricus castaneus* and *Eiseniella tetraedra* (154 and 150 mm³/g, respectively) take an intermediate position between that of *Dendrobaena octaedra*, and that of *Eisenia rosea* - *E. foetida*. Despite a relatively small number of replications (42 and 24), the respiration rate of both species significantly differs from that of both *Dendrobaena octaedra* and *Eisenia rosea*. When evaluating differences in the respiration rate of *Lumbricus castaneus* and *Dendrobaena octaedra*, the index of significance (t) is

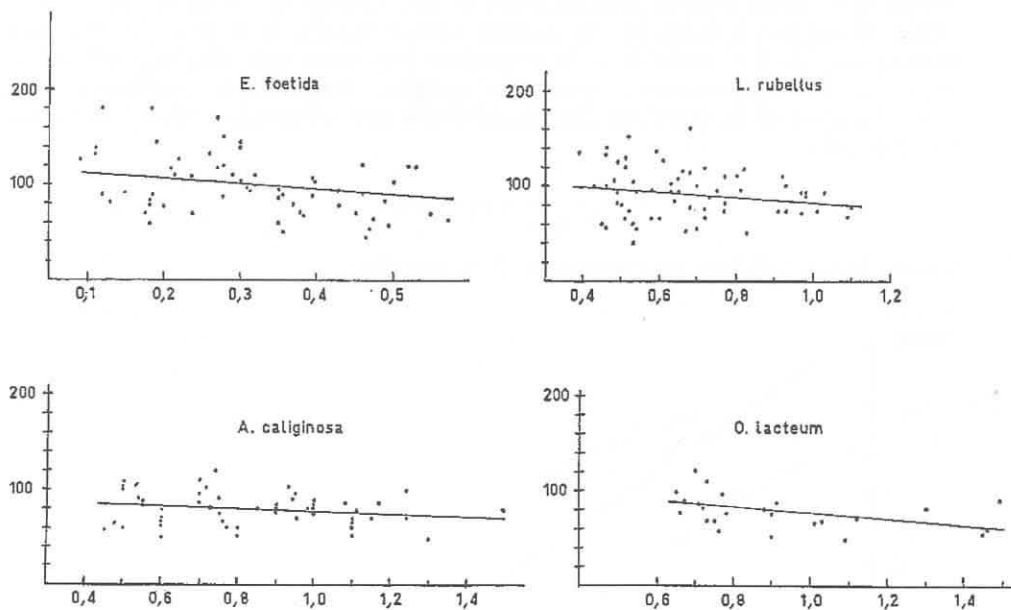


FIG. 3. — Continuation of Fig. 2, the same designations

equal to 4.7, being 8.8 in case of *Lumbricus castaneus* and *Eisenia rosea*, while at the level of significance $P = 0.01$ and $n = 29$ sufficient value of t is 2.76. For compared pairs *Eiseniella tetraedra* - *Dendrobaena octaedra* and *Eiseniella tetraedra* - *Eisenia rosea* t was 4.2 and 6.2, respectively ($t = 2.8$ being sufficient). In the second weight group the mean rate of O₂ consumption was the same in the individuals of *Allolobophora caliginosa* and *Octolasion lacteum*. Both species showed significant difference by this character from *Lumbricus rubellus*. The value of t was 2.75 at a comparison of data for *Allolobophora caliginosa* - *Lumbricus rubellus* ($t = 2.57$ being sufficient) while in comparison between *Octolasion lacteum* and *Lumbricus rubellus* t was 2.8, corresponding to the theoretical value of t at the level of significance of 0.01 and $n = 24$.

The fact that maximal weight fluctuations in mature individuals of each species were taken into consideration in the experiment gave the possibility to elucidate the respiration rate in relation to the body size of the worms. There were grounds to believe (cf. KRÜGER, 1952; SAROJA, 1959) that in worms, as well as in many other invertebrates (WINBERG, 1950, 1956) oxygen uptake is

in parabolic dependence upon the body weight. Corresponding curves actually show that in several species (*Dendrobaena octaedra*, *Lumbricus castaneus*, *L. terrestris*) the logarithms of the rate of O_2 consumption and the logarithms of body weight are rather in linear dependence. This allows to calculate O_2 consumption as function of the weight by the equation of the exponential curve.

$$Q = AW^b,$$

where Q — total oxygen consumption of the animal W — its weight, A — a value of oxygen uptake by an animal whose weight is a unit (in the same dimensions as W), while b — is a number less than unit showing the dependence of O_2 consumption upon the weight. From here, respiration rate (consumption of O_2 per hour calculated per a unit of weight) can be expressed by the ratio

$$\frac{Q}{W} = q = AW^{b-1}$$

where the coefficient of regression b is negative.

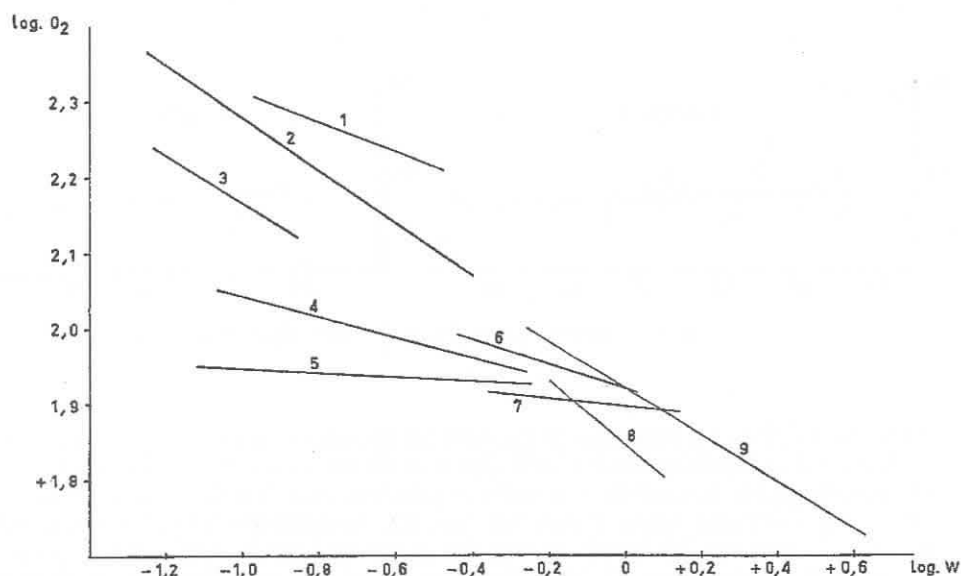


FIG. 1. — Dependence of O_2 consumption rate upon the weight in different Lumbricid species (Abscissa - logarithms of weight W ; ordinate - logarithms of O_2 consumption rate, q)

1. *Dendrobaena octaedra*
2. *Lumbricus castaneus*
3. *Eiseniella tetraedra*
4. *Eisenia foetida*
5. *Eisenia rosea*
6. *Lumbricus rubellus*
7. *Allolobophora caliginosa*
8. *Octolasion lacteum*
9. *Lumbricus terrestris*

Fig. 1 presents the dependence of the rate of O_2 consumption upon the weight of the worms. Coordinates of straight lines are calculated by the

least square method. *Dendrobaena octaedra* and *Eisenia rosea* show most drastic differences not only in the level of the rate of O_2 consumption but by its dependence upon the weight as well. In our tests the rate of O_2 consumption of *Eisenia rosea* did almost not decrease with the increase of the body weight ($b = -0.05$). A very small value of the coefficient of correlation (r) between the respiration rate and the weight (Table 2) reveals that this dependence, if existing, can be statistically proved at such a great variation in the values of individual data only at a much greater number of measurements than that has

TABLE II

Dependence of respiration rate upon the weight in different earthworm species

Species	Number of replications (n)	Coefficient of correlation (r)	Equation of resp. rate	Standard deviation (σ_b)
<i>Dendrobaena octaedra</i> (Savigny) ..	60	-0,45*	$q = 119 W^{-0,29}$	0,06
<i>Lumbricus castaneus</i> (Savigny) ..	42	-0,5	$q = 86 W^{-0,36}$	0,06
<i>Eiseniella tetraedra</i> (Savigny)	24	-0,42**	$q = 62 W^{-0,37}$	0,17
<i>Eisenia foetida</i> (Savigny)	60	-0,34	$q = 80 W^{-0,14}$	0,08
<i>Eisenia rosea</i> (Savigny)	65	-0,08	$q = 88 W^{-0,05}$	
<i>Allolobophora caliginosa</i> (Savigny).	50	-0,1	$q = 78 W^{-0,09}$	
<i>Lumbricus rubellus</i> Hoffmann	63	-0,22	$q = 93 W^{-0,16}$	0,13
<i>Octolasion lacteum</i> (Oerley)	24	-0,43	$q = 72 W^{-0,42}$	0,16
<i>Lumbricus terrestris</i> Linné	18	-0,9	$q = 83,5 W^{-0,29}$	0,05

*) Sufficient value of r at significance level of 0.01 (99 % of probability) makes 0.325.

**) The r value obtained exceeds that sufficient for significant level of 0.05 (95 % of probability).

been made ($n = 65$). Unlike this, *Dendrobaena octaedra*, at a similar number of replications ($n = 60$) and also strongly varying data of individual observations demonstrated a distinct reverse dependence of the respiration rate upon the weight coefficient of regression b making -0.29 . The absolute value of the coefficient of correlation ($r = 0.45$, $r = 0.33$ being sufficient), despite a large value of standard deviation ($\sigma_b = \pm 0.069$), suggests that this dependence is close to the actual one.

Eisenia foetida being close to *E. rosea* by the mean respiration rate, as mentioned above, differs from these latter by a distinct, although a less drastic than in *Dendrobaena octaedra*, dependence of the rate of O_2 consumption upon the weight. Similar calculations for *Lumbricus castaneus* and *Eiseniella tetraedra* show that even in case of a lesser number of observations a dependence of the respiration rate upon the weight is observed which is more or less close to that revealed for *Dendrobaena octaedra*. In the second weight group differences between species with respect to the character discussed are also observed. The dependence of the respiration rate upon the weight is very feeble in *Allolobophora caliginosa*. As well as in case of *Eisenia rosea*, a very low value of the coefficient of correlation suggests that respiration intensity decreases very little with an increase in the size, so that much more observations are required for the establishment of the regularity.

In *Lumbricus rubellus* the respiration rate decreases more sharply with an increase in the weight. *Octolasion lacteum* worms, despite a small number

of observations show a distinct and statistically significant dependence of the respiration rate upon the weight of the individuals.

A small number of measurements (18) was also carried out on *Lumbricus terrestris* worms, their weight ranging between 0.56 to 4.64 g. In the average the O_2 uptake was 74 mm³/g/h, the mean weight being 1.53 g. These data are similar to those obtained by JOHNSON (1942) who pointed out that at 16-17° C the respiration rate of these worms weighing 1.47 g was 70 mm³/g/h.

The mean respiration rate of *Lumbricus terrestris* is close to that of soil dwelling *Eisenia rosea* and *Allolobophora caliginosa*. However, as far as a can be judged by limited data, the rate of O_2 consumption in *Lumbricus terrestris* strongly falls with an increase in the weight, $b = -0.29$.

DISCUSSION

An analysis of the results of observations on the rate of respiration in Lumbricids differing in their ecology showed the possibility to discuss the data obtained from two viewpoints. First of all, high statistical significance of the difference between the mean rates of O_2 consumption in several species show that ecological differences are connected with differences in the metabolic level.

A more intensive metabolism is characteristic of litter dwelling and emerging on the soil surface pigmented worms if compared to non-pigmented soil dwelling ones. Thus, within the range of the first weight group *Dendrobaena octaedra* living at the surface is characterized by a higher rate of O_2 consumption than the soil dwelling *Eisenia rosea*. The same can be observed in general in the second weight group. The highest respiration rate of all the earthworms investigated was found in *Dendrobaena octaedra* which is an active animal, often the main destroyer of the litter in the forest zone (PEREL, 1963; GHILAROV, 1964). This worm is distributed far in the North, even in the shrub tundra where, under the conditions of low temperatures and short vegetation period it seems to be an ephemere. It should be noticed that pigmented species with a higher metabolic level in both groups penetrate further to the North than non-pigmented ones, such as *Eisenia rosea* and *Allolobophora caliginosa*. These latter have the lowest metabolic level of the species investigated. Of their ecological features the ability to aestivate during dry periods in an inactive rolled state should be stressed in this connection. Apart from this, *Eisenia rosea* individuals are able to survive temporary wetting and flooding of the soil. As shown by M. N. CHUGUNOVA (1957) *E. rosea* may live for a long time (460 days) in a small layer of stagnant water.

On the other hand, the above results demonstrate a different degree of the respiration rate dependence upon the worm weight. This dependence is the more distinctly manifested the higher muscular activity is characteristic of the worms. In highly active Lumbricids realizing relatively far horizontal and vertical migrations and being highly reactive to touching, a well pronounced reverse dependence of the rate of O_2 consumption upon the body size is revealed. To this group belong *Dendrobaena octaedra* and *Lumbricus castaneus*, soil-litter dwelling *Octolasion lacteum* and *Lumbricus terrestris*. Oxygen consumption of amphibiotic *Eiseniella tetraedra* sharply depends upon its weight as well. Coefficient of regression b is very close to -0.33 thereat

(or to 0.67 when analysing not the respiration rate $\frac{Q}{W} = AW^{b-1}$ but O_2 consumption by one worm, $Q = AW^b$) which suggests that in these active Lumbricids the respiration rate depends upon the respiratory surface of the body.

Unlike this, in typical soil dwelling non-pigmented *Eisenia rosea* and *Allolobophora caliginosa* which are less active and do not undertake rapid and considerable migrations, the respiration rate depends upon their weight to a very small degree.

The compost dwelling *Eisenia foetida* which is close to soil dwellers by the mean metabolic level shows, unlike them, a somewhat stronger manifested dependence of the respiration rate upon its weight.

SUMMARY

A comparative study of the respiration rate (O_2 consumption per g of wet weight per hour) in Lumbricids differing with respect to their ecology revealed that typical soil dwelling species *Eisenia rosea* and *Allolobophora caliginosa* have the lowest respiration rate. Soil-litter *Lumbricus rubellus*, *L. terrestris*, *Octolasion lacteum* and compost-dwelling *Eisenia foetida* are close to the former two species by this character.

The litter dwelling *Dendrobaena octaedra* shows the highest respiration rate, while the litter dwelling *L. castaneus* and amphibiotic *Eiseniella tetraedra* possess the intermediate place (closer to higher O_2 consumption group).

In 9 species of earthworm investigated a different degree of the dependence of the respiration rate upon the worm weight is found: with an increase of weight decreases at a different rate. Thus, in active living or in soil-litter dwelling species undertaking considerable migrations (*D. octaedra*, *E. tetraedra*, *L. castaneus*, *L. terrestris*, *O. lacteum*) this dependence is distinctly manifested but it is almost lacking in deeply living unpigmented, *Eisenia rosea* and *Allolobophora caliginosa* being less active. The compost dwelling species *Eisenia foetida* and soil-litter dwelling *L. rubellus* take an intermediate position in this respect.

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Adresse de l'auteur :

Ju. B. BYZOVA. — A. N. Svertzov Institute of Animal Morphology, Academy of Sciences of the USSR, Moscow, Vavilov Street 12/2, USSR.